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THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS, WITH SPECIAL REFERENCE TO SPECIES ISOLATED FROM MILK

I. REVIEW OF LITERATURE

A. H. ROBERTSON

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TECHNICAL BULLETIN NO. 130

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS, WITH SPECIAL REFERENCE TO SPECIES ISOLATED FROM MILK

I. REVIEW OF LITERATURE[1]

A. H. ROBERTSON[2]

ABSTRACT

Spore-forming thermophiles are widely distributed in nature. Physiologically and morphologically many of them resemble the common aerobic spore-formers and some investigators suggest that the former are derived from the latter by gradual acclimatization. Thermophilic actinomyces are common in nature also.

Only one non-spore-forming thermophile, *Lactobacillus thermophilus* Ayers and Johnson (1924b), has been described. Non-spore-forming species with unusual thermal resistance have been found among the streptococci, the sarcinae, and the lactic acid bacteria.

INTRODUCTION

Certain species of micro-organisms among the algae and bacteria, and less commonly among the molds and yeasts, have been found which are resistant to temperatures that are abnormally high for the existence of living protoplasm. Not only do the organisms survive, but in many cases they grow normally at and above 60° C. In this respect these forms differ from the normal species in these groups. Thermophilic bacteria normally belong to spore-forming types, tho non-spore-forming types have been described.

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[1]A portion of the thesis submitted to the Graduate School at Cornell University in partial fulfillment of the requirements for the degree of doctor of philosophy. The entire contribution appears in four parts, two of which, Technical Bulletins Nos. 130 and 131, are published by the New York State Agricultural Experiment Station, and two, Bulletins Nos. 274 and 275, by the Vermont Agricultural Experiment Station. The author acknowledges the many helpful suggestions offered during the course of the present investigation by Dr. R. S. Breed of the New York Station and by Dr. H. B. Ellenberger and Dr. B. F. Lutman of the Vermont Station.

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Sonnerat (1774)[3] first reported the existence of life at unusually high temperatures. According to an early statement, he saw living fish at 69° C in a thermal lake on the Island of Luzon, Philippine Islands. Wyman (1867) claimed that Sonnerat's observation was incorrect as determined by later visits to this lake.

A strictly thermophilic bacterium was first isolated from the Seine River by Miquel (1879). Miquel (1881, 1882, 1888) also was first to isolate thermophilic bacteria from soil and feces. The bacterial flora of canned goods was first investigated by Prescott and Underwood (1897, 1898) who probably failed to isolate any strict thermophiles.

The present work has been stimulated largely by Dotterrer's (1923) recognition of the presence of an unusually heat-resistant or thermophilic (heat-loving) flora in pasteurized milk. Soon after the World War, numerous laboratories engaged in milk control work began reporting the sporadic appearance of large numbers of small, punctiform, white colonies on agar plates. These so-called "pin-point" colonies were associated with pasteurized milk.

Fay (1927) has pointed out that the term "pin-point" colony may superficially characterize a number of different types of organisms as they grow on the agar plates. The term is quite unsatisfactory as it does not distinguish between the true thermophiles, the thermotolerant flora, and certain mesophiles, because several of these species under certain conditions may form punctiform colonies. The writer has observed spore-forming thermophiles whose colonies also might be considered "pin-point."

Usually public health officials, after observing the presence of this type of colony growth, advised the milk companies that some faulty operation had occurred at the plant which was responsible for the high bacterial count. When reports of similar conditions in several other cities in this country were given proper consideration, it was recognized that the cause of the "pin-point" colonies was not the result of so simple a thing as the failure properly to wash and sterilize the pasteurizing equipment. In some plants a series of samples were secured at different intervals during the pasteurization process which showed that the bacterial count of the milk increased during pasteurization.

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[3]Refers to Bibliography, Page 21.

The purpose of this investigation is to study the non-spore-forming, thermophilic and thermoduric species associated with milk. The results will appear in four parts as follows: I, a review of the literature on the thermophilic and related micro-organisms; II, a discussion of the heat resistance of micro-organisms; III, a description of the characters of the isolated organisms, some of which may frequently cause the "pin-point" colonies on the pasteurized milk plates; and IV, a report showing the effect of the age of the culture on the heat resistance of non-spore-forming bacteria.

Portions of the literature have been reviewed by Ambroz (1910), Noack (1912), Morrison and Tanner (1922, 1924), Krohn (1923), Tanner (1924b), Magoon (1926a), and Tanner and Harding (1926b). Therefore, under each classification by source only a short statement of the literature will be presented. The contributions will be reviewed according to the habitats from which the micro-organisms were isolated, as follows: (1) Milk, with special reference to bacteria; (2) waters, including fresh, thermal, and mineral; (3) feces, sewage, and heating manure piles; (4) soil; (5) canned goods; and (6) miscellaneous sources. The nature of certain contributions does not permit their being reviewed according to habitat. Therefore, they are considered in a separate section and because of their general scientific importance follow the preceding review of the literature on isolation according to habitat.

In order that there may be no misunderstanding of the terms applied to thermophilic and unusually heat-resistant bacteria, it is best to adhere to some classification. Usually macroscopic observation is the only means employed to detect optimum growth conditions. The classification is as follows: Strict thermophiles, optimum growth above 55°C and failure to grow below 37°C; facultative thermophiles, optimum growth between 45° and 55°C; thermotolerant species, optimum growth between 37° and 45°C; and thermoduric mesophiles, optimum growth between 20° and 37°C, but will survive in relatively large numbers in raw milk (at least 90 per cent survival) at temperatures as high as 62.8°C for 30 minutes.

The writer realizes that the term thermoduric mesophile will include some members of the genus *Lactobacillus*, some strains of *Escherichia coli* (Escherich) Castellani and Chalmers, and some so-called varieties of *Streptococcus lactis* (Lister) Löhnis, as well as many of the aerobic and anaerobic spore-forming group. High thermal resistance alone is not a character of sufficient importance to justify

establishing a new genus or species. Therefore, certain strains of some species are described merely as possessing thermoduric properties. A variety name or symbol is preferred unless there are two or more characters that distinguish the organisms in question from related forms.

THERMOPHILIC AND THERMODURIC MICROORGANISMS IN MILK

I. SPORE-FORMING SPECIES

Since the present work deals primarily with heat-resistant bacteria in milk, the literature will be discussed from this viewpoint, altho it is recognized that the original habitat of spore-forming thermophilic species is not the milk itself. The poorly washed milk utensils with the partially dried-on casein and albumin may be suitable places for the development of thermophiles. Also the dust from the air is a probable source of thermophiles.

That thermoduric spore-forming bacteria are common types in pasteurized, sterilized,[4] and boiled milk is well established by the studies of Hüppe (1884), Löffler (1887), Gruber (1888a, 1888b), Adametz (1890), Hesse (1890), Strub (1890), Petri and Maassen (1891, 1898), Pictet and Weyl (1891), Frankel (1893), Flügge (1894), Wróblewski (1895), Weber (1900), Dunbar and Dreyer (1900), Ferguson (1902), Rogers (1905), Knüsel (1908), Ford and Pryor (1914), Lawrence and Ford (1916), Laubach, Rice, and Ford (1916), Lisk (1924), and Robertson, Yale, and Breed (1926). The species found most frequently are members of the hay- and potato-bacillus groups.

Flügge (1894) was probably working with some of the thermophilic species, altho he did not recognize them as such. Leichmann (1894) was among the first to recognize that he had isolated a bacterium with thermophilic properties from milk. After heating the milk from 12 to 15 hours at 50°C, it coagulated, but the coagulum was different from that produced by typical strains of *Streptococcus lactis*. He isolated from this mass a slime-producing, facultative-thermophilic spore-former which grew best between 40° and 50°C. Rabinowitsch (1895) first isolated strict thermophiles from milk. Among the other workers who have isolated spore-forming thermophiles from milk and its products are Gorini (1895), Oprescu (1898), Weber (1900), Sames (1900), Schardinger (1903), Ambroz (1910),

[4]Term used in the practical sense.

Eckelmann (1917), Bergey (1919), Morrison and Tanner (1922), Tanner and H. G. Harding (1926a, 1926b), Clarke and Dougherty (1926), Eckford (1927) and H. G. Harding (1927). Because of the common characteristics possessed by all thermophilic spore-formers, a general description of the species in this group appears later.

II. NON-SPORE-FORMING SPECIES

That certain of the pathogenic staphylococci are more resistant to heat than other non-spore-forming pathogens has been established by the early work of Sternberg (1887), Van Geuns (1889), and De Man (1893), and more recently confirmed by Rosenau (1908), Patzschke (1916), and Park (1927). Hauser (1887) was perhaps the first to recognize the unusual heat resistance of some species of the micrococci. Adametz (1890) was among the first to observe sarcinae in sterilized milk. Dyar (1895) isolated a yellow micrococcus (probably a sarcina) from sterilized milk. Stubenrath (1897) studied sarcinae from other sources than milk and noticed their heat resisting properties. Hashimoto (1901) reported the isolation of micrococci from sterilized milk. Russell and Hastings (1902b) undoubtedly were studying a sarcina when they described a micrococcus, the thermal death point of which is 76°C in milk. Schweitzer (1903) observed the heat resistance of sarcinae in milk. Ayers and Johnson (1910, 1913) unquestionably had sarcinae among their acid-forming and alkali-forming groups which survived pasteurization. More recently Fenger, Cram, and Rudnick (1920) have shown that micrococci (probably sarcinae) occasionally survive in the heat treatment used in preparing surgical ligatures and sutures. In a preliminary report, the writer (1923) isolated some micrococci among which were sarcinae from pasteurized milk plates.

Marshall (1897) was among the first to observe the customary lactic acid fermentation in pasteurized milk similar to that occurring in raw milk. A sufficient number of the lactic acid bacteria survive the pasteurization process to produce normal lactic acid fermentation. Weiss (1899), Hashimoto (1901), Freudenreich and Thöni (1904), Rogers (1905), Adeloff (1907), Wolff (1908), Ayers and Johnson (1910, 1913), Shippen (1914), Hammer (1914), Gorini (1915, 1921), Peiser (1915), Brown and Peiser (1916), Weigmann, Wolff, Trensch and Steffen (1916), Patzschke (1916), Orla-Jensen (1919, (1921), Robertson (1923), Hammer and Baker (1923, 1926), and Fay (1927) have noted the thermal resistance of some of the lactic acid

species in milk. Ayers, Johnson, and Davis (1918) discovered that eight of their cultures of pathogenic streptococci survived 140° F for 30 minutes. A further study of these eight cultures showed that they could be distinguished from the other pathogenic species by certain cultural characters. Van Tieghem (1881), Hashimoto (1901), Lingelsheim (1912), Holman (1914), Bleyer (1923), and Johnson and Exworthy (1925) have isolated various streptococci, with unusual heat resistance, from milk or other substances. Beckwith and Eddie (1924) observed that hemolytic streptococci of human origin are not always killed by the pasteurization temperatures commonly used. Salter (1921) and Sears and Benson (1923) have reported similar findings. Several species of the genus *Lactobacillus* grow best at temperatures between 38° and 44°C (Bergey, 1923).

Colon bacilli with high thermal resistance have been observed by De Jong and De Graff (1906), Zelenski (1906), and Gage and Stoughton (1906). Ayers and Johnson (1915) studied the thermal death points of 174 cultures of *Escherichia coli* from one or more of the following sources: Human and cow feces, flies, cheese, milk, and cream.

Twiss (1920) reported that some of the colon and paratyphoid group survived pasteurization. Immediately Krumweide and Noble (1921) refuted this contention, suggesting that some error had been introduced into Twiss' work.

Greig-Smith (1909) and Downs (1925) have observed *Micrococcus albus* (Rosenbach) Buchanan frequently in condensed milk. Orla-Jensen (1919) reported the presence of sarcinae in sweetened condensed milk. Savage and Hunwicke (1923) have isolated micrococci most frequently from both sweetened and unsweetened condensed milk. Hunwicke and Jephcott (1925) have submitted data on the numbers and types of bacteria killed in the roller process of milk drying. Brannon and Prucha (1927) found two cultures which survived pasteurization among the 46 non-spore-forming organisms isolated. One of these was similar to Russell and Hastings' (1902b) organism. Among 21 non-spore-forming species which had been named before they were received at the laboratory, *Sarcina lutea* was found to survive the pasteurization temperature in milk.

Altho Jacobsen (1918), H. A. Harding (1923), Yates (1923), and Yates and Glover (1923) were probably dealing with a thermophilic flora in milk which they described as producing "pin-point" colonies on agar plates, Dotterrer (1923) first recognized the possibility of the development of a heat-loving flora in the pasteurizer with the in-

creased time of operation. Dotterrer took samples of milk from the holder at five-minute intervals when the same holder was used for five successive fillings. The plate count of the milk held at 143°F for 30 minutes indicated the normal reduction in the first filling only. In the other four fillings the count did not change much, altho in one case it was greater at the end than at the beginning of the holding period.

The work on this new "pin-point" flora of pasteurized milk has been reviewed by Tanner and H. G. Harding (1926) from the contributions by Ayers and Johnson (1923), Robertson (1923), Van Horn (1924), Taylor (1924a, 1924b), Hungerford and H. A. Harding (1924), Tanner (1924a), Adams and H. A. Harding (1924), H. A. Harding and Ward (1924), Ayers and Johnson (1924a, 1924b), and Swenarton (1925, 1926). The description of a new species, *Lactobacillus thermophilus* (Ayers and Johnson, 1924b), which grew best at pasteurizing temperatures explained one of the causes of "pin-point" colonies. The presence of "pin-point" colonies has been detected in the milk from individual producers and has been found both in certified and in medium and poor quality milk. More recently Clarke and Dougherty (1926) have confirmed some of the preceding observations on non-spore-forming thermophiles. Fay (1927) has described three types of thermo-tolerant saccharophilic organisms which form characteristic "pin-point" colonies.

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS FROM RIVERS, CANALS, AND HOT SPRINGS

I. BACTERIA

The earliest reference to a strictly thermophilic bacterium dates back to Miquel (1879) who attributed the property of thermal resistance to a different form of protoplasm. Prior to this Cohn (1875) isolated a facultative thermophile, *Beggiatoa nivea* Rabenhorst, from the sulfur springs at Aargau, Germany. Among the others who have isolated spore-forming thermophiles from similar sources are Certes and Garrigou (1886), Winogradsky (1887), Claassen (1888), Moniez (1893), Teich (1895), Pretti (1896), Kedzoir (1896), Miyoshi (1897a, 1897b), Davis (1897), Harshbarger (1897), Oprescu (1898), Michaelis (1899), Setchell (1903), Kehler (1904), Catterina (1904), Benignetti (1905), Skotschko (reviewed by Benignetti), Brazzola (1906), Andres (1906), Falcioni (1907), Tirelli (1907), De Kruijff (1909, 1910), Georgevitch (1910a, 1910b, 1911), Ambroz (1910, 1913), Nègre

(1913a, 1913b), Rössler (1918), Dufrenoy (1921), Morrison (1921), Morrison and Tanner (1922), and Elion (1924). Cantacuzène (1910) has demonstrated the presence of a thermophilic spirochete in the springs at Dax.

II. ALGAE

Hooker (1813) was among the first to note the presence of *Oscillariae* growing at 98°C in one of the thermal springs in Iceland. Fluorens (1846) also identified algae which came from an equally high temperature. Algae and related forms of plant life are frequently found growing naturally at temperatures ranging from 60° to 75°C in various thermal waters. Ehrenberg (1858), in addition to algae, has described motile rotifers, some members of the *Polygalaceae*, and living *Eunotia Sancti Antonii* at 63° to 65°C. Long (1822) reported the presence of numerous insects at the sides and bottoms of pools at 55.6° to 65.6°C. A small bivalve testaceous animal adhered to the plants and lived at these temperatures also. Among others who have observed thermophilic algae are James (1823), Agardt (1827), Corda (1835-36), Schwabe (1837), Meneghini (1843), Gervais (1849), Kützing (1849), Humboldt (1852), Stachey (1854), Hooker, J. D. (1854), Lauder-Lindsay (1861), Cohn (1862), Brewer (1866), Wyman (1867), Bickmore (1868), Hayden (1870-83), Lyman (1874, 1878), Parry (1874), Wood (1874), Dyer (1874), Moseley (1874), Hoppe-Seyler (1875), Archer (1875), Jones (1875), Skey (1877), Dana (1880), Serres (1880), Semper (1881), Junghühn (——), Griffiths (1882), Rogers (1884), Certes and Garrigou (1886), Perroncito and Varalda (1887), Hansgrig (1887), Nordstedt (1888), Kerner von Marilaun (1888), Weed (1887-88, 1889), Baring-Gould (——), Moseley (1892), Buscalione (1895), Pfeffer (1897-1904), and Lowenstein (1903).

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS IN FECES, SEWAGE, AND MANURE

Miquel (1888) isolated the first thermophile from feces. Others who have studied thermophiles from the above sources are Dehérain (1884), Globig (1888a, 1888b), Burrill (1889), Schlösing (1892), Rabinowitsch (1895), Macfadyen and Blaxall (1894a, 1894b, 1899), Baruchello (1897a, 1897b), Müller (1898), Herzberg (1899) Dupont (1902a, 1902b), Tsiklinski (1903), Bruini (1905), Skotschko (——), Anitschkow (1906), Bardou (1906), Ambroz (1910), Eckelmann (1917), Bergey (1919), Veillon (1922), Damon and Feirer (1925), and Greer (1926). Greer found that many of the common anaerobes could

grow rapidly at 50°C and a few could grow a little less abundantly at 55°C.

Miquel regarded the thermophiles in feces as unimportant, since their greatest activity occurred at temperatures above that of the human body. Anitschkow did not find the thermophiles common in the feces, but their presence could be easily demonstrated by enrichment methods.

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS IN THE SOIL

Miquel (1888) has priority in isolating thermophiles from soil also. Others who have found thermophiles in the soil are Globig (1888a, 1888b), Macfadyen and Blaxall (1894a, 1894b, 1899), Rabinowitsch (1895), Christen (1895), Cambier (1896), Baruchello (1897a, 1897b), Schillinger (1898), Oprescu (1898), Tsiklinski (1899a, 1899b), Sames (1900), Gilbert (1904), Benignetti (1905), Skotschko (——), Blau (1906) De Kruijff (1909, 1910), Ambroz (1910, 1913), Pringsheim (1911), Koch and Hoffmann (1912), Nègre (1913a, 1913b), Kroulik (1913), Eckelmann (1917), Krohn (1923), and Feirer (1927).

De Kruijff (1909), under tropical conditions, obtained atmospheric nitrogen fixation with thermophiles at 55°C. In the tropics, flasks of water reach a sufficiently high temperature during the day for the rapid growth of thermophiles. A maxium temperature of 62°C has been recorded. Spores of thermophiles when inoculated into bouillon grew during the middle of the day. At least nine hours during the day conditions are extremely favorable for decomposition by the spore-forming thermophiles. As the temperature approaches the maximum for the psychrophiles, their activity diminishes and simultaneously the activity of the thermophiles increases. At 11 o'clock in the evening a temperature of 48°C has been recorded for swamp water. Top soil temperatures favor the growth of thermophiles during the greater part of the day.

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS ASSOCIATED WITH THE CANNING INDUSTRY

The need for canned goods in this country was first felt during and immediately after the Civil War period, as indicated by the growth of the canning industry. For a long time success in canning was regarded as a mystic art. Later work has shown that the lack of

success in many cases was caused by the presence of thermophilic species which were not killed by the heat penetration. Duckwall (1899) submitted the first reliable treatise on bacteriology as applied to the canning and preserving of food products. Prescott and Underwood (1897, 1898) were perhaps the first to describe a group of species which they had isolated from canned goods. They found two species of micrococci and seven bacilli which were probably merely thermoresistant species. Russell (1895b) pointed out that underprocessing was the cause of a gaseous fermentation in canned goods. That canned goods often contained thermophiles was recognized by Ott (1904) and confirmed by Cathcart (1906).

A period of 14 years elapsed with few contributions, particularly in this country. Stimulated by the canning experiences during the World War, a deluge of new material, a large proportion of which treats of the causes and the methods of controlling spoilage, has been published. Only the important contributions will be mentioned.

Members of the hay- and potato-bacillus groups have been found most frequently in canned goods. New species, some of which are true thermophiles, have been described by Barlow (1912), Weinzirl (1919), Hunter and Thom (1919), Cheyney (1919), Esty and Williams (1919), Normington (1919), Donk (1919, 1920), Bunyea (1921), Wyant (1923), Wyant and Tweed (1923), Bitting (1924), Weinzirl (1924), Cameron and Esty (1925), and Fellers (1926). Molds, yeasts, actinomyces, sarcinae, streptococci, and micrococci have been isolated also.

THERMOPHILIC AND THERMODURIC MICRO-ORGANISMS FROM MISCELLANEOUS SOURCES

I. SILAGE

Burrill (1889), Albert (1893), and Griffiths (1894) have shown that the spore-forming thermophiles are associated with silage fermentation. Temperatures between 56°C and 70°C favor the formation of sweet silage. Ambroz (1910) found thermophiles in silage, but no data are submitted.

II. HAY

Cohn (1893a), Miehe (1906, 1907a), Dügelli (1906), Schütze (1908), Molisch (1908), and Miehe (1909) have isolated thermophiles from heating green hay. Boekhout and Ott de Vries (1908, 1909a) found that the heating was not wholly dependent on the thermophilic

species but instead was caused by an oxidation process catalyzed by the presence of iron.

III. COTTON

Zopf (1892), Haepke (1893), and Cohn (1893) have investigated the thermophiles in cotton. Zopf isolated a thermo-tolerant rod and Cohn found a heat-resistant micrococcus.

IV. TOBACCO

A number of investigators, among whom are Cohn (1893), Haepke (1893), Dávalos (1892), Behrens, (1894, 1896 1901), Koning (1897, 1898), Vernhout (1898, 1899), Loew (1899, 1900a, 1900b, 1901), Delacroix (1907), and Jensen (1908), have associated thermophiles with tobacco fermentations. Boekhout and Ott de Vries (1909b) clarified the uncertainty of tobacco heating by showing that it depended on an oxidation process activated by the presence of iron.

V. AIR, DUST, AND FILTH

Globig (1888b), Macfadyen and Blaxall (1894a, 1894b, 1899), Rabinowitsch (1895), Sames (1900), Bardou (1906), De Kruijff (1909), and Bergey (1919) have isolated thermophiles from dust and air.

VI. BREAD

The sliminess of improperly baked bread has been investigated by Laurent (1885), Kretschner and Niemslowicz (1889), Uffelmann (1890), Russell (1898), Vogel (1897), Eckles (1899, 1902), Juckernach (1900), Thomann (1900), König and Spickermann (1902), Budinoff (1903), Fuhrmann (1906), Ambroz (1910), and Kaiser and Delaval (1911). During the baking of bread, the maximum temperature is usually not over 105°C. Probably certain substances in the bread aid in retarding the passage of water into the cell. *Bacillus panis* (Vogel) Migula has been isolated most frequently. Other species which have been isolated commonly are members of the hay- and potato-bacillus groups.

Cohn (1893) and Rabinowitsch (1895) found thermophiles in grains. The heating of meal has been investigated by Zopf (1892), Holliger (1902), Levy (1904), Maurizio (1906), and Teichert (1907). Schardinger (1903, 1907) isolated them from cereal and from stuffed foods, such as sausages and frankfurts. Laxa (1898, 1900), Poŭpě (1898), and Kosscowicz (1912, 1913) have found them in sugar solutions. Ambroz (1910) associated a decomposition of hyacinth bulbs with a thermophilic growth. Sames (1900) described a thermophile associ-

ated with certain discharges from the human body. Greig-Smith (1921) isolated a thermophile from fermenting tan-bark. Cohn (1893) associated thermophiles with the heating of hops.

PAPERS OF GENERAL SCIENTIFIC INTEREST

Göbel (1923) obtained a higher survival of *Bacillus pyocyaneus* Gessard cells in a bouillon suspension than in a physiological salt suspension when they were subjected to the same temperatures. The lower the dilution of the organisms, the greater was the percentage of the organisms surviving. In other words, the resistance of the individual cell in a dilute suspension was greater than in a concentrated suspension.

Bleyer (1923) heated cultures of streptococci at 50°, 56°, 60°, 65°, 70°, and 80°C for one hour in a water bath. After inoculating the heated cultures into the blood stream of white rats, he recovered streptococci in a number of cases from the liver, spleen, and heart blood.

Behrens (1923) maintained that there was an optimum concentration of cells above or below which a greater percentage of killing occurred when the culture was subjected to high temperatures. Oerskov (1925, 1926) found that the older cultures, i. e., 24 hours old versus freshly inoculated (not more than 2 to 3 hours old), were more resistant to heat.

Eijkmann (1908) was first to show the "S" shape of the rate-of-killing curve when bacteria were subjected to temperatures approaching their thermal death point. Just (1877) observed the germination of seeds after exposure to high temperatures after heating in dry air and in liquids. Porodko (1927a, 1927b) has presented additional data on the rate of killing of seeds by heat and their ability to germinate afterwards. Boycott (1919) obtained S-shaped curves for the rate of killing of multicellular organisms (tadpoles) when subjected to heat.

Tanner and Wallace (1925) obtained the growth curves of three species of thermophilic bacteria at 20°, 37°, and 55°C in plain broth. At 20°C the growth was irregular and not as rapid as at 37° or 55°C. No definite peak in the curve was obtained. At 37°C the period of maximum growth was reached in from 16 to 30 days. At 55°C growth was very rapid, many of the cells dying soon after the period of active growth had passed. Cells of thermophilic species growing at 55°C wear themselves out quickly, the cultures often becoming sterile.

Preheating the medium to 55°C before inoculation always shortened the lag phase of growth. At 55°C the lag phase was from three to four hours long when inoculated with old cultures but was almost eliminated when inoculated with rapidly growing cultures.

Koser (1927) has demonstrated a bacteriophage which is active against a thermophilic species. Golikowa (1926) reported that the thermophilic species can adapt themselves to unusual temperature conditions. The characteristics of the various species isolated are unstable. Group agglutinins for thermophiles could be developed in dog serum.

Most bacteriologists agree that the thermal death points of bacterial species must be expressed in some form of temperature-time relations. That thermal resistance was dependent on the nature of the medium containing the bacteria was perhaps first demonstrated by Von Esmarch (1888) and has been confirmed by later investigators.

Buchanan, Thompson, Orr, and Bruett (1918) submitted a formula for determining the temperature at the center of a can of food during the process of sterilization. The formula may be applied at any time except during the first few minutes. Bruett (1919) found that blanching was not an effective method of killing the spores in canned goods. Burke (1919) first called attention to the delayed germination of spores after they had been heated. Bigelow and Esty (1920a, 1920b) first pointed out that the initial number of spores influenced the time required for sterilization. They confirmed the work of Buchanan *et al* (1918) on the influence of the free hydrogen-ion concentration on the heat resistance of the spores.

Considerable variation has been observed in the thermal resistance of different strains of the same species as well as different concentrations of the same strain by Shanly (1915), Esty and Williams (1919), Dickson, Burke, and Ward (1919), Dickson, Burke, Beck, Johnson, and King (1922), and Esty (1923). Some workers attribute this to a higher resistance of a few cells, since more than 95 per cent of the cells are killed in a relatively short time at an exposure just below their maximum thermal resistance. Burke (1923) explained this property by the probable impermeability of the cell wall to water.

Differences in the rate of heat penetration in the processing of canned foods were first pointed out by Bigelow (1920) and his collaborators, Bohart, Richardson, and Ball. These differences depend

on the nature and consistency of the contents of the cans, variation in the size of the can, the initial temperature, the retort temperature, and the cooling and heating methods. Bigelow and Cathcart (1921) called attention to the wide variations in the pH values for individual canned foods and to the changes in the pH values during processing.

Dickson, Burke, and Ward (1919) found that the addition of 5 per cent lemon juice to the medium did not prevent the formation of toxin by *Clostridium botulinus* Van Ermengen (1896) but did lower the thermal death points. Bigelow (1921) in his studies on the processing of canned goods first used the logarithmic thermal death time curves to express the rate of death of the organisms when heated.

Magoon and Culpepper (1921) summarized some of the factors affecting the penetration of heat into cans as follows: (1) Size of vessel, (2) ability of the container to radiate heat, (3) concentration of the sugar or starch within the container, (4) mobility of the contents of the container, (5) mobility of the heating and cooling medium, and (6) the shape of the container.

Esty and Cathcart (1921), reporting on the influence of hard and soft pyrex glass tubing for heating cultures, found that unbuffered solutions caused considerable change in the pH. Heating mixtures of Na_2HPO_4 and KH_2PO_4 in hard glass tubes did not affect the hydrogen-ion concentration during the heating, while prolonged heating in soft glass tubes dissolved out alkali in excess of the amount which could be controlled by the buffer salts. Heating in alkali solution of this mixture in soft glass caused a greater lowering of the hydrogen-ion concentration than acid solutions. A neutral solution did not change appreciably during the heating, even in soft glass tubes. Heating juices of canned vegetables in soft glass tubes affected the pH less than in hard glass tubes.

Magoon and Culpepper (1922) pointed out that some of the variations in thermal resistance of micro-organisms in canned foods was dependent on variations in the initial temperature of the substances in the cans and the pressures and vacuums within the cans. Weiss (1921a) found that young moist spores were more resistant than old ones, and that spores one month old were three times as resistant as those five months old. Esty and Meyer (1922) reported that young moist spores, probably those of the first generation, appeared to be the most resistant. Magoon (1926a) found that older spores were more resistant than the young ones. Among some of the fac-

tors influencing the heat resistance of spores were the humidity and the temperature at which the spores were held.

Tanner and Dack (1922) found that the spores of *Clostridium botulinum* survived much higher temperatures when exposed to dry heat than have been reported for its resistance to moist heat, as reported by Weiss (1921b). Tanner and McCrea (1923) observed that a longer time was required to destroy the spores of *Clostridium botulinum* of the same age in open tubes than in tubes exhausted and sealed. After Burke (1923), Esty (1924) recognized the presence of especially heat-resistant individuals in the spore suspensions. Their presence explains the skips which occur when a series of tubes containing the same suspension of spores is subjected to the same heat treatment at a temperature in the proximity of their thermal death point. Hastings, Fred, and Carroll (1926) suggested that the presence of skips and stops could be partially overcome by the use of proper methods. Some modifications were the use of a neutral heating medium, a uniform cell suspension, the absence of contamination in the heated cultures, and perfect conditions for growth after the heat treatment.

Weinzirl (1924) showed that aerobic spore-formers when inoculated into sterile meat and incubated at 37°C never produced typical putrefaction. Anaerobic spore-formers were regarded as responsible for the typical putrefaction of meat. Starin (1926) found that the spores of *Clostridium botulinum* tended to lose not only their viability but their toxigenic powers also when subjected to heat. Viljoen (1926) observed a protective action exerted by sodium chloride in concentrations up to 4 per cent on bacterial spores in heated pea liquor.

GENERAL DESCRIPTION OF SPORE-FORMING THERMOPHILES

Before summarizing the distribution of the various species according to their habitats, a brief statement of the characters of the spore-forming thermophiles is given. The rods may be long or short, thick or slender, motile or non-motile, Gram positive or negative, mostly non-capsulated, and are arranged singly, paired, or in chains. Thread forms are rather common. Roeser (1890) showed that the typhoid bacilli assume long thread shapes when grown at their maximum temperatures. Aerobes, facultative anaerobes, and strict anaerobes are found. The spores may be either central or terminal and oval

or round. The growth on agar may or may not be luxuriant and may or may not be pigmented. Usually the growth is dull white or brownish. Carbohydrates are usually fermented, but gas may or may not be formed. Gelatin may or may not be liquefied. Nitrates may or may not be reduced to nitrites and ammonia. Milk may or may not be coagulated and peptonized. Starch is usually hydrolyzed. Usually the species are not pathogenic. Indol and hydrogen sulfide are sometimes formed. Frequently growth does not occur on the agar and potato slants.

The above description might just as well be applied to the common spore-forming species. Dupont (1902) has shown that *Bacillus subtilis* (Ehrenberg) Cohn and *B. mesentericus ruber* Globig grow at 50°C. Blau (1905) found that the spores of *B. subtilis* germinate at 60°C after a long time. After 48 hours at 55°C the spores of *B. subtilis* formed thin grayish-yellow colonies. *B. parvus* Neide (1904) also grew under similar conditions in 24 hours. *B. megaterium* De Bary (1884) and *B. subtilus* grew at 50°C. After 48 hours at 50°C, *B. ruminatus* Gottheil (1901) produced incipient signs of growth. Greer (1926) found that many of the anaerobic spore-formers grew at 50°C and a few could grow at 55°C.

Rabinowitsch (1895), Schillinger (1898), and Tsiklinski (1903) regarded the thermophiles as merely varieties of the common non-thermophilic species. These species were simply thermo-tolerant, since they had adapted themselves to new temperature conditions (Schillinger.) Because of their resistance to adverse conditions and their power of adaptibility, they are found widely distributed in nature. Tsiklinski believed that the facultative thermophiles would become strict thermophiles if continually grown at high temperatures. A facultative thermophile would merely be an intermediate stage. Eckelmann (1917) has demonstrated a partial loss and recovery of the ability to resist heat among some of her thermophiles. After growing in liquid media, their heat-resistance decreased, but after growth on solid media for a long time their former heat resistance was regained.

DISTRIBUTION OF SPECIES DESCRIBED BY PREVIOUS WORKERS

Spore-forming thermophilic rods can be associated with all the sources which have been considered, i.e., milk, water, feces, soil, canned goods, silage, and various fermenting organic materials. Mi-

crococci are more frequently associated with milk and its products. Some workers have found them in canned goods. Less commonly they have been found in unsterile surgical sutures and ligatures, fermenting cotton, and in water in which beans have been boiled.

Thermophilic actinomyces have been found by Globig, Karlinski, Rabinowitsch, Kedzoir, Tsiklinski, Sames, Bruini, Gilbert, Miehe, Schütze, Nègre, Velich, Bergey, Lieske, Krohn, and Eckford. Isolations have been made from one or more of the following places: Soil, fresh water, sulfur springs, sewage, manure, fresh feces, milk, canned goods, hay, air, and the Sahara sands.

Thermophilic species are not uncommon in mineral springs. Cohn, Certes and Garrigou, Winogradsky, Karlinski, Teich, Falcioni, Miyoshi, and Dufrenoy have isolated thermophiles from sulfur springs. Hoppe-Seyler, Miyoshi, and Dufrenoy have found them in water containing iron.

Bardou (1906) and Ambroz (1913) have described denitrifying species. Elion (1924) described a sulfate-reducing thermophile. Pringsheim (1913), Kroulik (1913), and Viljoen, Fred, and Peterson (1926) have found thermophiles associated with the destruction of cellulose. Thermophiles in soil, manure, and fermenting green fodders are quite likely to be cellulose fermenters.

Anaerobic thermophiles have been isolated by Oprescu (1898), Tsiklinski (1903), Nègre (1913a), and Veillon (1922). More recently Greer (1926) showed that many of the common anaerobes could grow rapidly at 50°C. Nègre concluded that all obligate thermophilic bacteria were obligate aerobes and that facultative thermophiles were facultative aerobes, a statement with which other investigators do not agree.

DISTRIBUTION OF LIFE WITH REFERENCE TO TEMPERATURES

MacDougal (1921) and MacDougal and Working (1921) have reported a most interesting observation on the high temperature record for endurance and growth in *Opuntia*. In the second paper a temperature of 56.5°C in the tissue and 58.0°C for the air was reported. Bates and Roeser (1924) showed that variation in the resistance of tree seedlings to excessive heat was dependent on the lack of moisture in the soil to maintain turgor and the seedlings tipped over at the ground line. Certain trees, and naturally also their seedings, are better adapted thru their root systems to over-

come the lack of moisture in the surface soil of semi-arid, hot regions. Sachs (1864) observed that plants were killed at an air temperature of 51°C in 10 to 30 minutes, while 45° to 46°C in water kills them in 10 minutes.

The distribution of life according to temperatures has been well summarized by Davenport and Castle (1895). The *Protista* have the highest maximum temperature of any group, it being above 60°C for active organisms in water. The *Ciliata* show the decidedly low temperature of 42°C. Among the *Metazoa*, the highest maxima recorded are 44° and 45°C for some insects (Plateau, 1872). For the great majority of the *Metazoa* the maximum temperature lies between 30° and 40°C. The green algae are less resistant than the blue-green algae, the maximum temperature for the former being about 70°C and for the latter about 80°C. Probably some of the blue-green forms can survive the boiling temperature of water.

SUMMARY

The literature on thermophilic and thermoduric micro-organisms has been reviewed. Spore-forming thermophiles are widely distributed in nature. They have been isolated from the following habitats: Thermal springs, fresh waters, canal waters, sewage, fresh animal and human feces, infant feces (one to five days old), cultivated and uncultivated soil (particularly garden soil), market milk, canned goods, heating manure piles, fermenting malt, meal, bran, hay, cotton, tobacco, silage, tanbark, hops, grains, and the "fullmasse" of sugar solutions. Ordinarily they are not common, but their presence can easily be demonstrated by enrichment methods.

Physiologically and morphologically they resemble the common aerobic spore-formers. Some investigators suggest that the property of unusual thermal resistance has been acquired by the aerobic spore-forming species and that after the acquisition of this new character they are recognized as thermophiles. Natural conditions probably induce certain of the species with the greatest powers of adaptability to modify their existence and gradually to take on new properties such as growth at higher temperatures. Thermophilic actinomyces have also been isolated from a variety of sources.

Only one non-spore-forming thermophile, *Lactobacillus thermophilus* Ayers and Johnson (1924b), has been isolated. Milk is the only recognized source of this species at present. Non-spore-forming species with unusual heat resistance have been found among the

streptococci, the sarcinae, and the lactic acid bacteria. The unusual thermal resistance of a few strains of *Escherichia coli* has been noted.

The highest temperatures at which life exists has been observed among the algae and has been recorded as 98°C. Thermophilic bacteria grow best between 55° and 75°C. The maxium temperatures for the *Metazoa* are 44° to 45°C.

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